



Seasonality in Frequency of Marine Access to an Intermittently Open Estuary: Implications for Recruitment Strategies

K. N. I. Bell^{a,b,c}, P. D. Cowley^a and A. K. Whitfield^a

^aJ. L. B. Smith Institute of Ichthyology, Private Bag 1015, Grahamstown, 6140 South Africa

^bDepartment of Ichthyology and Fisheries Science, Rhodes University, Grahamstown 6140, South Africa

Received 31 December 1999 and accepted in revised form 17 August 2000

Timing of life-history stages and environmental conditions is key to recruitment success. We examine the seasonal pattern in access between the surf zone and an estuary, and the implications for recruitment success and process in fish that spawn at sea but spend their juvenile phase in estuaries. About 70% of South African estuaries are closed by barrier sand bars that open intermittently; an alternative but brief access opportunity is marine overwash (overtopping), when the surf zone extends over the bar to contact estuarine waters. Larval fish have limited ability to wait for an access opportunity (overtopping or opening event), so timing of settlement is important with respect to the seasonal distribution of waiting times for access opportunities. Periodic regression on daily observations (1993–1999) at the East Kleinemonde Estuary profiled the seasonal variation in expected waiting time. The data set is dominated by overwash events. Waiting time (for all events) is significantly related to both the first and second harmonics of season, and tends to be longest in December–January, and shortest in April–May. If the analysis is restricted to openings alone waiting times are shortest near November, and longest from February to September. The seasonal variation shown has implications for recruitment processes, population sizes, and productivity in estuaries. © 2001 Academic Press

Keywords: seasonal cycles; periodic regression; waiting time; bar-built estuaries; overwash; overtopping; fish larvae; recruitment; migration; residence time; mortality; South Africa

Introduction

The timing of developmental stages with respect to the temporal distribution of critical opportunities affecting survival is acknowledged to be a key factor in recruitment (Cushing, 1990). A number of marine-spawning fish species are regarded as dependent on estuaries in South Africa (Whitfield, 1998), with spawning and the very early life-history in the marine environment, and an intermediate portion of the life-history in estuaries. It is thus critical for completion of the life-cycle that the larvae of estuarine-dependent fish (in this paper referred to simply as ‘fish’) can enter estuaries.

Entry of larval fish into estuaries can occur only when there is either a clear passage to the sea (open), or when waves sweep over the barrier bar (overwash). The latter effectively is an expansion of the surf zone such that it meets the estuary proper. Entry of fish larvae to estuaries during overwash events is a newly-recognized phenomenon (Whitfield, 1992b, 1998; Cowley *et al.*, submitted).

Larvae are stages with limited swimming ability and limited energy reserves. These constraints imply a strong survival benefit to optimal timing of arrival in the surf zone near dates which have the shortest waiting times until the next opportunity to enter the estuary.

The East Kleinemonde estuary is categorized as intermittently open, or temporarily open/closed (Whitfield, 1992a, 1998). About 70% of South African estuaries are of this type. To facilitate precise discussion of estuary accessibility states, we apply the following terminology:

Estuarine access opportunity (EAO) is either via (1) Estuary Mouth Opening (EMO or ‘opening’), or (2) a Bar Overwash Event or overtopping event (BOE or ‘overtopping’).

Incomplete overtopping (IOT) is an event in which the surf zone advances toward the estuary but does not meet it (during these events, larvae sometimes are trapped in temporary pools and die). Potential access from surf zone to estuary on each day can be categorized on the basis of whether there is an Estuarine

^cTo whom correspondence should be addressed. E-mail: K.Bell@ru.ac.za

Access Opportunity (EAO) or not, or quantified by how much later the next EAO occurs.

Waiting time (WTM) is the number of days from any date to the next EAO, i.e. $WTM = \text{day}_{\text{EOA}} - \text{day}_i$. Because WTM is applicable to any calendar date in a series, it is a way of accommodating all these estuarine events together in analysis.

EAO data, such as that of Cowley (1998) for East Kleinemonde, suitably analysed, can improve the understanding of the seasonal constraints on recruitment. We hope to demonstrate from the East Kleinemonde example that such data can be used to generate predictive relationships. The prime objective of analysis is to generate an objective description of EAO periodicity that will allow evaluation of whether a seasonal pattern in the EAOs relates to seasonal pattern in the presence of recruitable fish in the surf zone. Insight may thus be afforded into the selection forces that have formed the temporal recruitment (to surf zone, to estuary) patterns exhibited by fish. Such insights may also inform conservation strategies. A relationship could indicate that the seasonal structure of EAOs in intermittently open estuaries has been a factor in the selection for timing of events leading to recruitment. A failure to positively relate could indicate either the presence of other stronger factors favouring different times, or it could indicate that the timing may correspond better to the EAO opportunities in other types of estuaries, for example intermittently open estuaries with higher frequencies of opening than East Kleinemonde.

This paper therefore describes the pattern of EAOs at Kleinemonde, and compares the pattern in overwash with the pattern in openings (complementary subsets of EAOs).

Materials and methods

Bar overtopping and estuary mouth opening data

Data on estuarine access opportunities at the East Kleinemonde estuary were collected on an ongoing basis from March 1993 to May 1999.

EAO status was recorded for each day in four categories: (1) no overwash and estuary closed; (2) wave overwash of duration <3 h (i.e. only at the highest quarter of the tidal cycle); (3) 3 to 6 h (one quarter to one-half of the tidal cycle); and (4) estuary open. No differentiation was made between single and multiple occurrences within one day of overwash types (2) and (3). In the analysis no differentiation was made on account of the duration, within each day, of an opening or overwash.

These data were transformed into a set of data representing for each day in the series the waiting time (waiting time in number of days) to the next EAO event, i.e. waiting time until the next opportunity for larvae to transit from the surf zone to the estuary. For analyses restricted to one type of EAO (i.e. either overwash or opening), the waiting time is the time to the next EAO of the same type. Waiting time was then analysed for its relation to the annual cycle.

Periodic regression (Bliss, 1958; Batschelet, 1981; Bell *et al.*, 1995; Bell, 1997) was applied to waiting time (dependent variable) in relation to the independent circular or periodic x variable representing time of year. Periodic regression is unfamiliar to most biologists, yet extremely useful for the analysis of cycles, so a brief explanation is given in Appendix A.

Effect of waiting time (WTM) variation on cohort survival

The effect of seasonal pattern in waiting time on cohort survival was modelled using the well-known relation:

$$N_t = N_0 e^{-Zt} \quad (1)$$

where N is numbers at time t , e^{-Z} (Ricker, 1975) here represents daily survival rate ($S = N_{t+1}/N_t$), and t in this context is waiting time in the surf zone or WTM.

We used equation 1 with the empirically derived waiting time values and a range of values for time-specific S , to include the plausible values for daily survival rates, from 0.99 to 0.8. N_0 used was 100 000 per day. For each value of S we generated a seasonal pattern, composed of, for each day in the year, the calculated number of survivors out of a cohort that recruited to the surf zone that day to recruit after the waiting time to the estuary. Time-specific survival (S_{daily}) was held temporally constant in each model, so no variation in S plays any part in the patterns seen. Because the effect of time is to exponentiate survival ($0 < S < 1.0$), the proportional variation in survival, due to cycling WTM over the seasonal cycle, increases as time-specific survival declines from 1.0. Note that the model output is the size of the remnant of each cohort, which is the appropriate measure to assess relative success due to differential timing, and from which to infer selection direction; what is found in the surf zone will be the sum of the remnants of all cohorts.

Results

Preliminary visualization of the data (Figure 1) indicates much variation over time in the waiting time observed, the most extreme being the presence in this

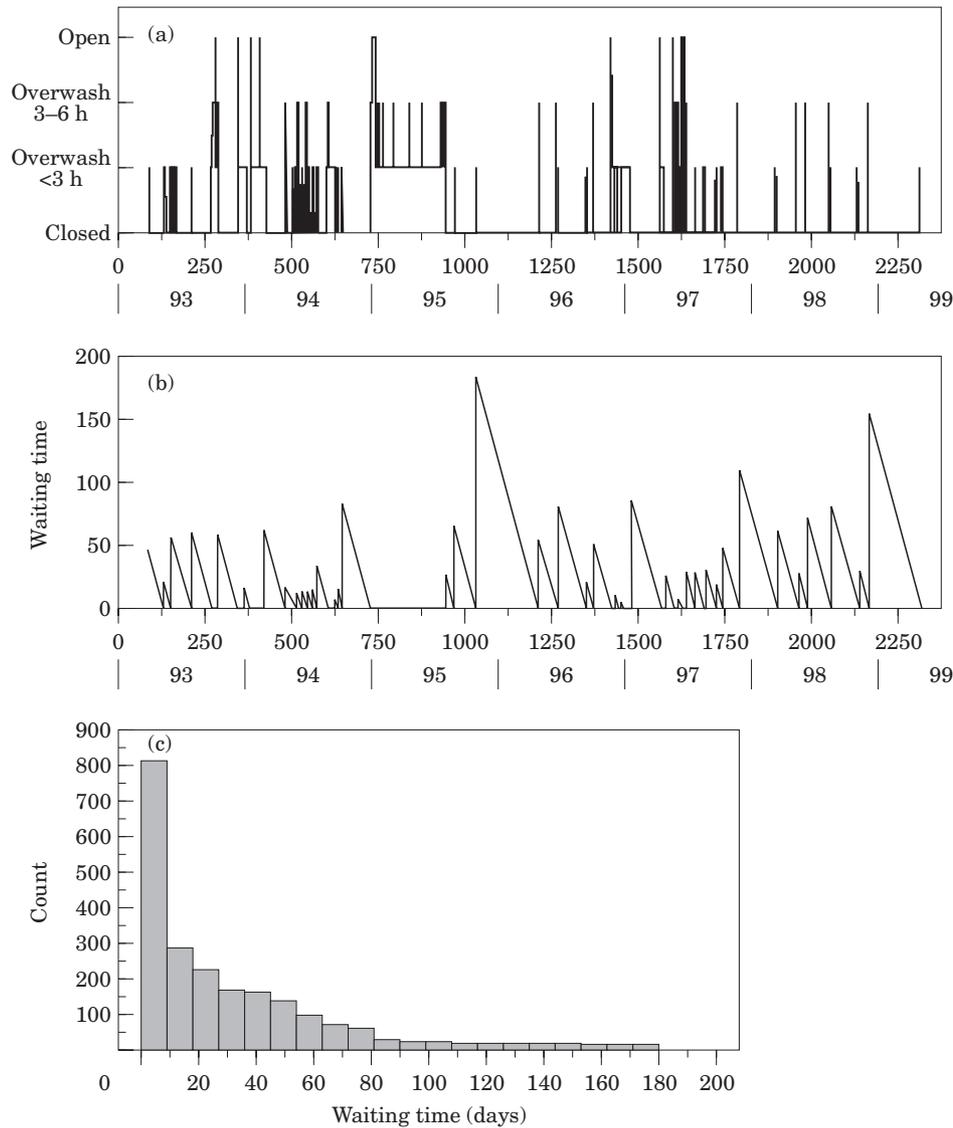


FIGURE 1. Opening and overwhelm incidence: (a) conditions plotted over entire series 1993–1999; the x -axis is labelled with sequential days since 1 January, 1993 and the year; (b) Trajectory of waiting time over entire series; (c) Frequency histogram of waiting times.

series of one (possibly anomalously) long and continuous series of EAOs virtually filling the first half of 1995. Anomalous appearances notwithstanding, no dates were excluded from the analysis.

Cycles in waiting times

For most questions, there are a number of subtle variations. In analysing waiting times, the variations important here are firstly whether those waiting times are analysed as individual data or as averages, and secondly the type of EAOs included in calculating waiting times.

The waiting times are analysed as (1) individual observations ($WTM_{\text{individual}}$), or (2) averages over all years for each date so that there are averages for each month and day ($WTM_{\text{date-averaged}}$) to make up what could be called an average year. These reflect two subtly different forms of the question, both equally legitimate. It should be obvious that data analysed on an individual basis tends to show much lower correlations (R^2) than the same data to which some kind of averaging has been applied (Central Limit Theorem). Though the approaches yield very different correlations, the functions that result are virtually indistinguishable.

TABLE 1. Seasonal component (principal and first harmonic cycles) of individual (1993–1999) waiting time on each day until the next EAO opportunity. Periodic regression coefficients for waiting time (WTM) against time of year expressed as sine and cosine of angular transforms of day of year (DOY). Transformation to angular units is indicated by ‘R’ and the second harmonic is indicated by a following ‘h’. Parameter significances are given in a row below coefficients. Relative contribution of each cycle to total variation can be determined from the amplitude (‘Ampltd’), which is in units of y . Regression overall significance and peak locations are given in columns to the right. Peaks are the locations (x -values) where the contribution of cyclic x -functions to y are greatest; ‘Peak’ relates to the primary cycle; ‘2ndHPeaks’ relate to the second harmonic. These models assume symmetry so that minima are displaced from maxima (peaks) by one-half cycle; i.e. displaced 6 months for primary cycles (first harmonic) and 3 months for second harmonic. The regression form is:

$$y = B_0 + B_1 \sin(R'DOY) + B_2 \cos(R'DOY) + B_3 \sin(R'hDOY) + B_4 \cos(R'hDOY)$$

	B_0	12-month cycle		6-month cycle		R^2	N	P	Peak	2ndHPeaks
		B_1	B_2	B_3	B_4					
All EAOs (Overwash and opening events together)										
WTM=	30.003	-4.644	+18.969	+1.264	+7.035	0.16	2056	0.0001	18 Dec	6 Jan, 7 Jul
	$P=$	0.0001	0.0001	0.2369	0.0001					
	Ampltd		39.04		14.28					
WTM _{avg} =	30.020	-4.695	+18.914	+1.341	+7.133	0.842	365	0.0001	17 Dec	6 Jan, 7 Jul
	$P=$	0.0001	0.0001	0.0051	0.0001					
	Ampltd		38.96		14.52					
BOEs (Overwash only)										
WTM=	30.507	-4.364	+18.227	+1.458	+7.411	0.16	2232	0.0001	18 Dec	6 Jan, 8 Jul
	$P=$	0.0001	0.0001	0.142	0.0001					
	Ampltd		37.5		15.1					
WTM _{avg} =	15.92	-4.246	+13.356	-1.972	+3.726	0.771	365	0.0001	14 Dec	17 Dec, 18 Jun
	$P=$	0.0001	0.0001	0.0001	0.0001					
	Ampltd		28.02		8.43					
EMO (Open only)										
WTM=	220.219	+63.441	-32.908	+48.09	-6.887	0.322	1353	0.0001	30 Apr	19 Feb, 21 Aug
	$P=$	0.0001	0.0001	0.0001	0.338					
	Ampltd		142.86		97.16					
WTM _{avg} =	305.23	+73.930	-60.999	+74.109	-3.553	0.857	365	0.0001	12 May	17 Feb, 18 Aug
	$P=$	0.0001	0.0001	0.0001	0.1741					
	Ampltd		191.7		148.38					
RAINFALL (Monthly totals only)										
RAIN (mm)=	54.258	-7.178	+20.261	na	na	0.114	54	0.046	12 Dec	na
	P	0.3935	0.0193	(was n.s.)	(was n.s.)					
	Ampltd		42.98							

We present both individual waiting time and date-averaged waiting time approaches because in our opinion the understanding of the tradeoffs within the recruitment process is in its infancy and can benefit from a diversity of approaches.

We also analysed separately the waiting time patterns for all EAOs, overwashes alone, and openings alone.

All regressions (whether for all EAOs or a subset, and whether for waiting times as individual or date-averaged data) were highly significant ($P \approx 0.0001$; Table 1, Figures 2, 3) in both the primary cycle and the second harmonic (6-month cycle). Because the second harmonic may account for considerable variation, the primary peak and minimum waiting

time may not exactly equal the aggregate peak and minimum; the aggregate is best read from the graphs.

As appealing as high correlations are, in fact the suitability of either model depends on the application. The meaning of the correlations on individual data or date-averaged data is subtly different; for example for WTM_{EAO} , the R^2 of 0.16 means that 16% of the variation in $WTM_{individual}$ is accounted for by the regression, while the R^2 of 0.84 means that 84% of the variation in the $WTM_{date-averaged}$ for that date over 6 years is accounted for. Choice of form depends on the question, i.e. whether the interest is in the long-term or short-term tradeoffs available, or to individual fish or to the species. From the point of view of an individual fish awaiting an EAO, the higher

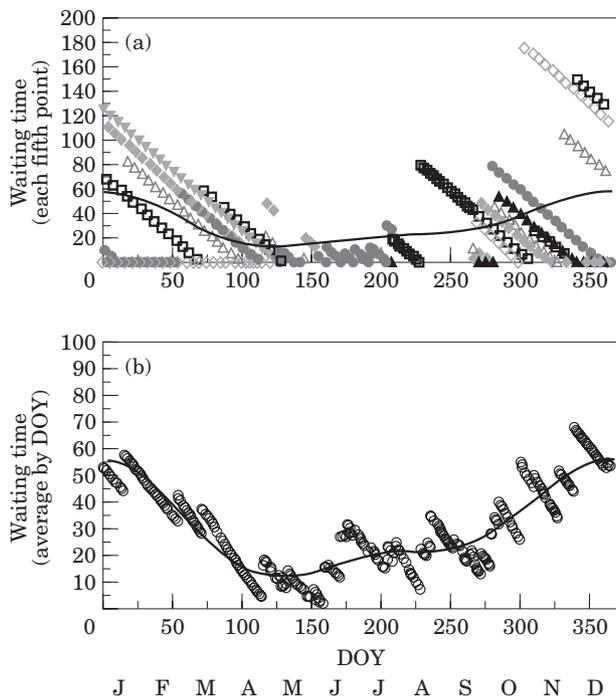


FIGURE 2. Seasonal pattern in waiting times for both kinds of EAO (opening or overwash) combined (1993–1999). Regressions are given in Table 1. WTM for overwash alone is not shown because overwashes dominate in EAOs and WTM_{BOE} is extremely close to the pattern for all EAOs. For clarity only each fifth point is plotted. (a) Individual waiting times with regression line; (b) Date-averaged waiting times, with regression line. \blacktriangle 1993, \bullet 1994, \diamond 1995, \blacklozenge 1996, \triangle 1997, \square 1998, \blacktriangledown 1999.

unpredictability of the individually-based analysis may be more germane; for a population under long-term selection, the date-averaged analysis may be more instructive.

All EAOs. Waiting times were significantly related (Figure 2, Table 1) to both the first and second harmonics of the annual cycle. WTM tends to be longest in December–January, and shortest in April–May. As anticipated, the correlations are less strong in the individual-date analysis than in the date-averaged analysis.

Using $WTM_{individual}$ data the regression is significant ($R^2=0.16$, $N=2056$, $P<0.0001$); using $WTM_{date-averaged}$ data the regression is also significant ($R^2=0.84$, $N=365$, $P<0.0001$), but the R^2 is much increased (Figure 2, Table 1). The regression coefficients differ little between the individual-days and date-averaged models. Residuals from the individual-WTM approach show a shape that clearly results from the structure of the data, i.e. reaching but not passing through zero. Residuals from the date-

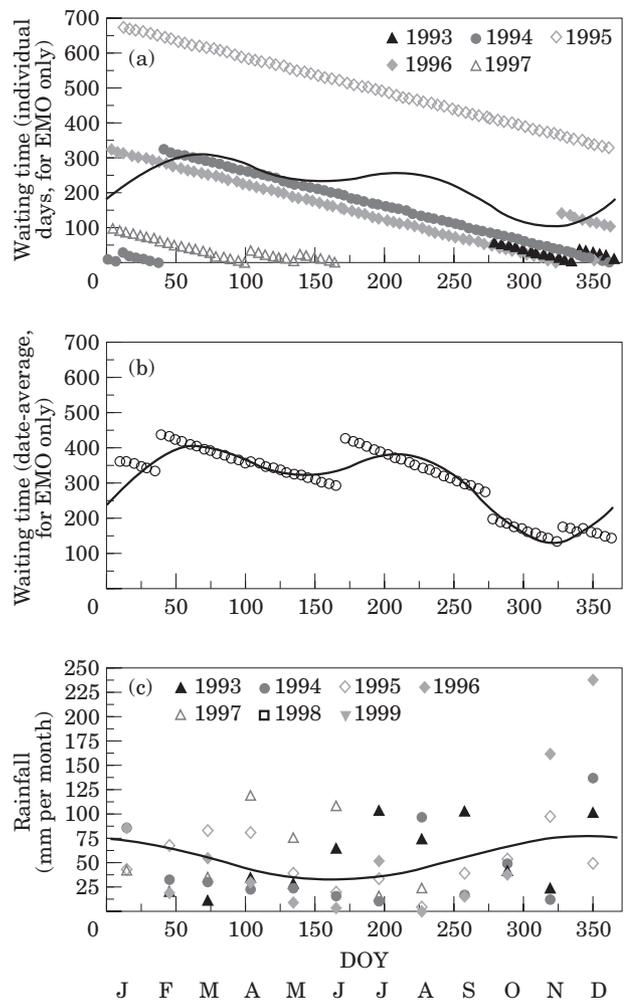


FIGURE 3. Seasonal pattern in waiting times for only the openings (EMOs) component of EAOs, and rainfall (1993–1999). Regressions are given in Table 1. (a) WTM_{EMO} for individual days. (b) Date-averaged WTM_{EMO} ; (c) Rainfall (mm per month).

averaged model are much better behaved in terms of normality. Residuals from both models are without apparent trend with respect to x .

The indicated maximum waiting time (the worst time for an arriving recruit) is in mid-December, the minimum (best time to recruit) in early May.

Overtoppings alone. The pattern showed by WTM_{BOE} contains highly significant primary and second harmonic cycles (Table 1). The regression for individual waiting times is highly significant ($R^2=0.16$, $N=2232$, $P=0.0001$) and indicates a peak contribution, i.e. longest waiting time (worst recruitment opportunity) from the primary cycle at 18 December and peak contributions of the secondary harmonic at 6 January and 8 July. The best recruitment opportunity is most

likely to occur at the shortest waiting times, and because the fitted function is symmetrical the minimum contributions of each cycle are displaced one-half cycle from the maximum: the minimum periodic contributions to waiting time therefore occur at 18 June (primary cycle or first harmonic), and 9 April and 6 October (second harmonic).

Openings and precipitation. The pattern shown by openings alone (Table 1, Figure 3) contains highly significant primary and second harmonic cycles, whether on an individual waiting time basis (primary peak 30 April, $R^2=0.32$, $N=1353$, $P=0.0001$) or a date-averaged waiting time (primary peak 12 May, $R^2=0.86$, $N=365$, $P=0.0001$). The peaks are within days of each other for either the individual WTM or the date-averaged WTM.

Rainfall, expressed as mm per month, shows a pattern that is significant at $P<0.05$ (Table 1, Figure 3) with an implied peak at 12 December.

Effect of waiting time variation on cohort survival

For plausible (0.85 to 0.95) daily survival rates for larval fish, the implied seasonal variation in recruitment (i.e. remaining survivors) after WTM_{EAO} reaches four orders of magnitude at $S_{daily}=0.8$, and for WTM_{EMO} alone the seasonal variation is over four orders of magnitude even at $S_{daily}=0.95$ (Figure 4). The peak survivals occur for all EAOs in early May and for openings in mid-November.

Discussion

It is widely accepted that there are fish species that have an apparently obligate estuarine phase, e.g. *Rhabdosargus holubi*, which are abundant as juveniles and sub-adults in intermittently open estuaries such as the East Kleinemonde (Cowley & Whitfield, submitted). The odds of success for such species depend on the availability of opportunities for larvae to transit the barrier bar either during overwash seas or mouth openings, and enter estuaries while minimizing mortality due to predation (cumulative over time, or waiting time) or starvation.

Intermittent openings and overwashes are features that define a grouping of South African estuaries as intermittently open, also called 'temporarily open/closed' (Whitfield, 1992a). Yet, for estuaries which are for most of the time closed, entry is in the short term highly unpredictable as it relies either on floods or high seas. If there is any predictability, any pattern, over the long term, it would be reasonable to explore the implications for the optimal behaviour of individual fish or populations.

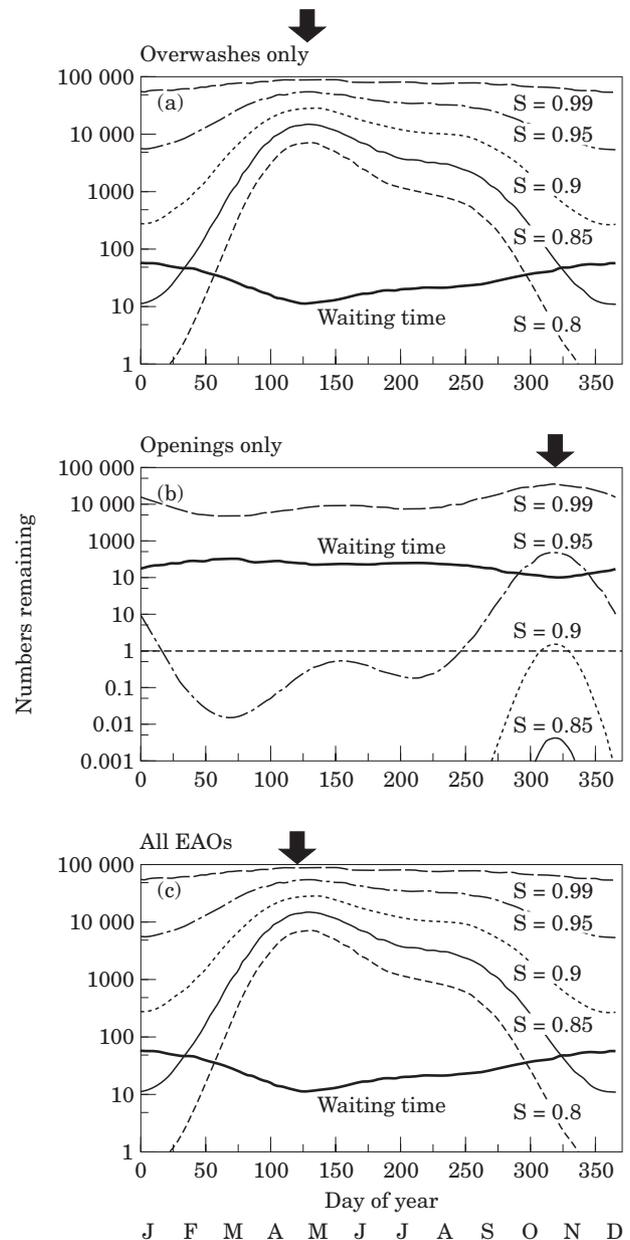


FIGURE 4. Implications of waiting time for recruitment at East Kleinemonde. Survivors from 100 000 fish after effects of mortality over the waiting time predicted from pattern of (a) overwashes alone; (b) openings alone (cumulative survival is too small for $S_{daily}=0.8$ to show); and (c) all EAOs (i.e. combining openings and overwashes). Equation applied is the standard $N_t=N_0e^{-Zt}$, where WTM is put in for t , 100 000 is put in for N_0 , survivals of 0.99 to 0.80 are put in for e^{-Zt} , and WTM is that derived from regression equations in Table 1. The y-axis units are numbers of fish remaining for the curves showing survival, and days for waiting time. Arrows mark dates that maximize survival. Graphs (a) and (c) are similar because overwashes are much more frequent than openings.

The peak opportunity from the waiting time aspect is obviously where the shortest occurs. The shortest

waiting time affords an individual fish the greatest flexibility to enter the estuary based on growth, energetic and developmental reference points, or based on an age-growth relationship (Bell *et al.*, 1995) that is exceeded (enter) or not (delay entry). The variation in the time required (WTM) will necessarily interact with prevailing mortality rates to yield further variation in recruitment and recruitment success.

Waiting times vary from zero to hundreds of days. They show temporal patterns that differ depending on whether all EAOs, or just overwashes, or just openings, are considered. The analysis most appropriate to East Kleinemonde is of course the one containing all kinds of EAOs that were recorded there. However, analysis of overwashes and openings separately shows that they contain different patterns; these patterns may be either generalized or appropriate to particular estuaries. The distribution of EAOs is the key to their effects on recruitment: although there are many in the series, because they are temporally clustered they facilitate recruitment much less than if they were more spaced out.

Cycles in waiting times

All EAOs. Waiting time (WTM) at East Kleinemonde shows very clearly ($P \approx 0.0001$) an effect of an annual cycle (with a half-year harmonic) in the observed waiting times. The equations for the individual-date and the date-averaged data are both very highly significant ($P \approx 0.0001$) and have virtually identical peak location dates and amplitudes; the only difference is in the R^2 , which as expected is much higher in the date-averaged analysis ($R^2 \approx 0.84$, compared with $R^2 \approx 0.16$ for the individual-date analysis).

The overall EAO pattern at East Kleinemonde is essentially stable whether it is based on all EAOs or overwashes only. However, it shows a radically different pattern from openings on their own. Overwashes are thus the most important form of EAO at East Kleinemonde.

Overwashes alone The pattern shown by overwashes contains highly significant primary and second harmonic cycles (Table 1), and is very similar to the pattern of all EAOs at East Kleinemonde, indicating the dominance of this type of EAO. The regression using averaged waiting times shows virtually the same pattern, but of course has a much higher R^2 (0.77).

Openings and precipitation The pattern shown by openings (EMOs) is very different from that shown by overwashes (BOEs). The data set is dominated by overwashes, but if these are excluded to consider the

openings alone (EMOs), indicated shortest waiting times are near November, and the longest are from February to September (Table 1, Figure 3). The peak WTM_{BOE} is in mid-December, while WTM_{EMO} peaks in April–May.

Rainfall is thought to be the main driver of the EMO seasonal pattern. Openings are expected to occur when rainfall causes estuarine water levels to rise more quickly than the barrier bar can grow, so it seems reasonable that the highest rainfall should coincide with the shortest WTM_{EMO} . The implied peak rainfall (12 December) coincides with the shortest WTMs as implied by the pattern of EMOs, supporting this link.

EMO patterns in estuaries with higher freshwater flows (or larger watersheds) may show similar patterns of seasonality but with higher mean frequencies than East Kleinemonde. If such estuaries are common, then the EMO pattern could be as important as the overwash pattern, and would tend to select for recruits that settle into surf zones in late November.

That the data come from a single location does of course limit generalization of these results. The data set is moderately long (6 years), but not long enough to allow access to longer-term variations that may on a decadal scale alter seasonality itself. The watersheds feeding estuaries like the East Kleinemonde have been subject to alterations including water removal; how this has affected the local EAO pattern is not known.

Effect of waiting time variation on cohort survival

The periodic regressions indicate a strong seasonality in the expected waiting time until an EAO, whether including all EAO data or restricting to overwashes. This seasonality has strong implications for recruitment strategy and its investigation. (This interestingly is an example of the kind of situation that would include a Bell-Doppler recruitment (Bell, 1997) component that would be recruit-date referenced, and would also include recruitment pulsing caused by sustained periods during which $d(\text{age at recruitment})/dt = 1$, [as in Figure 1(b)].)

Most generally, selection would be expected to favour reproductive phasing that maximized fitness, so reproduction should be expected to be phased so as to introduce recruits to the surf zone at the time when entry to estuaries is most likely and when the waiting time and consequent cumulative mortalities are minimized. Assuming other constraints like time-specific mortality rate in the surf zone to be temporally invariant, the selection attractor is the predicted

minimum waiting time (Figures 2, 3). This is in early May (if considering all EAOs) or mid-November (if considering openings alone).

How important is it for fish to time recruitment to the surf zone with the minimum waiting times? The maximum overall survival occurs for those cohorts arriving near the minimum waiting times, and this benefit increases as time-specific mortality rate in the surf zone also increases. Plausible daily survival rates for larval fish are included in the range 0.8 to 0.95. The implied seasonal variation in remaining survivors after W_{TMEAO} (waiting time for either type of access) reaches four orders of magnitude at $S_{daily}=0.8$, and for W_{TMEMO} (waiting time for mouth openings only—this means longer waiting times) the seasonal variation is over four orders of magnitude even at $S_{daily}=0.95$ (Figure 4). (W_{TMBOE} i.e. for overwash events only, will be similar to W_{TMEAO} because overwash predominates in EAO events.) This level of variation in success is large and would be expected, to the extent that response to appropriate cues is heritable, to feed back through selection. Of course, all selection pressures together form an aggregate for any characteristic, and this particular source may be balanced by others acting to favour different spawning and recruiting times.

The model (from the pattern in these cohort remnant sizes) predicts that the best time for larvae to enter the surf zone and attempt to enter estuaries like East Kleinemonde is near early May (pattern for either all EAOs or overwashes alone) or mid November (openings alone), and that survivorship falls off very rapidly for fish arriving earlier or later (Figure 4).

We do not necessarily expect that, as assumed in the model, the supply of larvae settling into the surf zone is temporally constant. The varying waiting time is real for at least the current EAO data, and survival is a process generally held to act as modelled. This simple model, by illustrating what would happen if reproductive effort were temporally constant shows why reproductive effort should in fact be expected to vary seasonally in response to the varying survival prospects.

Under those constraints, the conclusions are straightforward and mathematically unavoidable. If, for example, a factor like time-specific survival (S_{daily}) showed a seasonal or other pattern, it could be readily added to the model to yield a revised implied optimal time for recruitment to (or settlement into) the surf zone, i.e. lack of fit of observations with expectations from any model would provide evidence of the presence of other factors, and may facilitate their detection and assessment.

Empirical data would throw more light on how fish behave with respect to the implied minimum waiting time. Such data include recruitment rates from the plankton to the surf zone, mortality rates in the surf zone, availability for recruitment of larvae in the surf zone, and recruitment rates from the surf zone to the estuary.

Seasonal patterns in fish presence and EAO

The analysis of EAO data for the East Kleinemonde estuary shows that April–May are the most auspicious in terms of estuary accessibility (Figures 2, 4). Yet fish are present in the surf zone of East Kleinemonde for much of the year, with a significant peak for *Rhabdosargus holubi*, the dominant species, in August (Cowley *et al.*, submitted). As commented in that paper, the abundance peak is within the period of lower waiting times and higher projected survivals [plateau in Figure 4(a or c)]. The peak in August is thus consistent with the survival expectations from waiting times, where overwashes are included in the calculation. The prospects for fishes which cannot take advantage of overwash seem comparatively bleak [Figure 4(b)], because with openings only the waiting times are much longer and cumulative survivals indicated are in the <1% range unless unrealistically low time-specific mortality rates are assumed. What then is implied by the presence of larvae in the surf zone at times of year other than the waiting time minimum? This could reflect one or more of the following:

- (1) the ends of a seasonal distribution in reproduction that matches the seasonal minimum in expected waiting time for an EAO at this estuary;
- (2) that fish have evolved with responses appropriate to less disturbed systems that might naturally open with greater frequency than they now do with the existing abstraction of fresh water;
- (3) that responses are suited to the situation farther north where openings are more frequent and timed with rainfall;
- (4) the relative insignificance to the population of this estuary or closed estuaries;
- (5) the lack of correspondence of the present data to the longer-term average situation to which these species are exposed;
- (6) that fish stay only briefly near this estuary while they are moving along the coastline until an EAO is encountered, for example in a perennially open estuary;
- (7) environmental variation in time-specific survival rates or other factors such that the waiting time minima are not the sole contributors to selection for recruitment timing.

To give insight into the tradeoff of the mortality risk against the variation in availability of other alternatives, these hypotheses can be addressed by the following:

- (a) initiation of data sets similar to the EAO dataset collected at East Kleinemonde
- (b) sampling over time of the surf zone concurrent with incomplete overwash (and also full overwash) sampling;
- (c) relative frequency over time of successful *vs* unsuccessful (stranding) estuary entry;
- (d) sampling of fish entering the nearest open estuaries along the same coast and determination of ages of fish (from incomplete overwash strandings and from surf zone);
- (e) growth and survival in intermittently open estuaries, compared to those that are always open.

Are estuarine-dependent marine spawners a unique category?

This paper was intended to raise questions as much as answer them. Often, particular groupings of fish and questions concerning them are considered in isolation, because they appear unique on account of habitat and life-history. However, whatever uniqueness is perceived is not necessarily a reason to avoid the application of general principles and the making of comparisons.

Recruitment to estuaries appears to involve at least a two-part process: settlement out of the plankton and occupation of the surf zone until an EAO occurs or is found, and then recruitment to the estuary. But is this unique? Reef fishes (Victor, 1986b, 1986a; Wellington & Victor, 1989, 1992) also have a pelagic stage and presumably risk failure to be carried to suitable settlement sites, and may face competition or exclusion that has an unpredictability similar to that posed by EAOs. Sicydiine gobies (Manacop, 1953; Fourmanoir, 1954; Aboussouan, 1969; Erdman, 1984; Aiken, 1988; Radtke *et al.*, 1988; Bell & Brown, 1995; Bell, 1997) have a marine postlarval period, and risk failure to make their way to coastlines and rivers, and face intense predation on entry to rivers. Predation appears there to be dealt with by predator swamping, as several disparate groups (from fish to crustaceans) recruit together in phase with the lunar cycle (Bell, 1994). The episodic nature of EAOs may confer on recruits entering estuaries like East Kleinemonde some degree of predator-swamping advantages, as seen with sicydiine gobies. However, during the surf zone residence period prior to entry predator swamping would require that cohorts arrive in pulses and complete their transit quickly.

In light of these few comparisons, for the purposes of understanding estuarine fish recruitment, these fishes probably should not be considered a 'special' group in isolation. Instead, comparisons amongst diverse species and groups should be exploited where possible to increase understanding of fundamentals.

Conclusion

The seasonal component to waiting time at the East Kleinemonde estuary is strong, and has implications for recruitment processes, population sizes and productivity in estuaries. The implication for cohorts experiencing this seasonal variation in waiting time in the surf zone is that there are large costs, in terms of survival reduced to one tenth, or reduced to one thousandth, in consequence of arriving and having to wait through the longest waiting times (late December). Much information of relevance to the recruitment question is, however, unknown, e.g. how fish arbitrate the waiting time cycle, what seasonal pattern exists in their arrival to surf zones, what the mortalities are in surf zones, whether they commit themselves to a particular estuary or rove the coastline until finding an EAO.

The method applied here to identify, record and analyse the EAOs can be applied to other estuaries to facilitate comparison of their temporal behaviours. By the suggestions offered, we hope to encourage the pursuit of this knowledge.

Acknowledgements

We gratefully acknowledge the JLB Smith Institute and Rhodes' Department of Ichthyology and Fisheries Sciences for hosting this work, the National Research Foundation for Science Liaison funding to one of us (KNIB), the Hugh Kelly Fellowship at Rhodes University (KNIB), and colleagues for discussions and encouragement.

References

- Aboussouan, A. 1969 Note sur les Bichiques de l'île de la Réunion. *Recueil des Travaux Fasciales Hors Series, Supplement—Station Marine d'Endoume* 1969(9), 25–31.
- Aiken, K. A. 1988 Notes on the ecology of fishes of some rivers in Poland. *Natural History Notes of the Natural History Society of Jamaica* 2, 9–19.
- Batschelet, E. 1981 Circular statistics in biology. In *Mathematics in Biology* (Sibson, R. & Cohen, J., eds). Academic Press: London, xvi+371 pp.
- Bell, K. N. I. 1994 Life cycle, early life history, fishers and recruitment dynamics of diadromous gobies of Dominica, W.I.,

- emphasising *Sicydium punctatum* Perugia. Ph.D. thesis, Memorial Univ. of Nfld. St. John's, Nfld., Canada A1B 3X9. xviii+275 pp.
- Bell, K. N. I. 1997 Complex recruitment of dynamics with Doppler-like effects caused by shifts and cycles in age-at-recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 1668–1681.
- Bell, K. N. I. & Brown, J. A. 1995 Active salinity choice and enhanced swimming endurance to 0 to 8-d-old larvae of diadromous gobies, with emphasis on *Sicydium punctatum* (Pisces), in Dominica, West Indies. *Marine Biology* **121**, 409–417.
- Bell, K. N. I., Pepin, P. & Brown, J. A. 1995 Seasonal, inverse cycling of length- and age-at-recruitment in the diadromous gobies *Sicydium punctatum* and *Sicydium antillarum* (Pisces) in Dominica, West Indies. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 1535–1545.
- Bliss, C. I. 1958 Periodic regression in biology and climatology. *Bulletin of the Connecticut Agricultural Station, New Haven* **615**, 1–55.
- Cowley, P. D. 1998 Fish population dynamics in a temporarily open/closed South African estuary. PhD thesis, Rhodes University. Grahamstown. 145 pp.
- Cowley, P. D. & Whitfield, A. K. (submitted) Fish population size estimates from a small closed estuary in South Africa, using mark-recapture and density extrapolated techniques. *Marine and Freshwater Research*.
- Cowley, P. D., Whitfield, A. K. & Bell, K. N. I. (submitted) The surf zone ichthyoplankton adjacent to the mouth of an intermittently open estuary in South Africa, with evidence of recruitment during marine overwash events. *Estuarine and Coastal Shelf Science*.
- Cushing, D. H. 1990 Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology* **26**, 249–293.
- Erdman, D. S. 1984 The freshwater goby, *Sicydium plumieri*, and the goby fry fishery in Puerto Rico. *Fishbyte* (Newsletter of Network of Trop. Fisheries Scientists, published by ICLARM, MC PO 1501, Manila) **2**(1), 19.
- Fourmanoir, P. 1954 Ichthyologie et pêche aux Comores. *Mémoires de l'Institut des Sciences du Madagascar* **A**, 187–239.
- Manacop, P. R. 1953 The life history and habits of the goby, *Sicyopterus extraneus* Herre (aŋga) Gobiidae with an account of the goby-fry fishery of Cagayan River, Oriental Misamis [Province, Mindanao, Philippines]. *Philippine Journal of Fisheries* **2**, 1–60.
- Radtke, R. L., Kinzie, R. A. & Folsom, S. D. 1988 Age at recruitment of Hawaiian freshwater gobies. *Environmental Biology of Fishes* **23**, 205–213.
- Ricker, W. E. 1975 Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* **191**, xviii+382 p.
- Victor, B. C. 1986a Delayed metamorphosis with reduced larval growth in a coral reef fish (*Thalassoma bifasciatum*). *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 1208–1213.
- Victor, B. C. 1986b Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). *Marine Biology* **90**, 317–326.
- Wellington, G. M. & Victor, B. C. 1989 Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). *Marine Biology* **101**, 557–567.
- Wellington, G. M. & Victor, B. C. 1992 Regional differences in duration of the planktonic larval stages of reef fishes in the eastern Pacific Ocean. *Marine Biology* **113**, 491–498.
- Whitfield, A. K. 1992a A characterization of southern African estuarine systems. *South African Journal of Aquatic Science* **18**, 89–103.
- Whitfield, A. K. 1992b Juvenile fish recruitment over an estuarine sand bar. *Ichthos* **36**, 23.
- Whitfield, A. K. 1998 *Biology and Ecology of Fishes in Southern African Estuaries*. Ichthyological Monographs of the J. L. B. Smith Institute of Ichthyology, No. 2, iii+223 pp.

Appendix

Periodic regression (excerpted with permission from K. N. I. Bell teaching notes)

Periodic regression is a simple adaptation of ordinary regression to situations where one or more x -variables are cyclic or periodic (e.g. compass headings, time of year, time of day). In practice it is multiple regression carried out on trigonometric functions of angular transforms of periodic x -variables. The intersection of a cylinder by a planar surface describes a sinusoidal curve on its circumference. The sinusoidal curve is therefore the simplest function to apply to a linear-periodic relation.

The procedure fits a sinusoidal curve to data, and significance levels and correlations are obtained as for any multiple regression. It is analogous to plotting the data on a clear cylinder of circumference representing the cycle, e.g. 365 days of a year, and then rotating the cylinder until the strongest possible relation is identified in the view from a point at right angles to the axis of the cylinder (demonstrated in [Figure 1](#) of Bell, 1997). The amount of rotation from the (arbitrary) zero is a fitting of one parameter and worth 1 degree of freedom (d.f.). The regression can be fitted iteratively, in which case this d.f. must be kept in mind when determining significance, or it can be fitted explicitly using sin and cos functions of the time of year after transformation to angular units. In the explicit method the d.f. are taken care of by the two parameters (sin and cos). There is no restriction in principle on which angular system is used, but radians are the units most commonly required by computer programs and the azimuthal or compass-like system is the convention we use here. In representation, a circular or periodic variable occupies two dimensions, which can be represented by sines and cosines. Therefore, the x -variable, e.g. time of year expressed as day of year (DOY: 0–364·99), is first transformed by multiplying DOY by $2\pi/365$ to convert to radians. The resulting variable ($R'x$, here $R'DOY$) is decomposed into both a sin and cos, which become the pair of proxy variables representing DOY or time of year. The regression then takes the form:

$$y = B_0 + B_1 \sin R'DOY + B_2 \cos R'DOY + \varepsilon \quad (1)$$

where B_0 is an intercept, other B s are parameters, and ε represents a normally distributed error. Note that the sin and cos parameters together represent the periodic variable, so they should not be separated; even if one is not significant it cannot legitimately be dropped without dropping the other also. Three

concepts important to periodic regression are (1) mesor, (2) peak, and (3) amplitude. The intercept in periodic regression is not properly interpreted as the value of y where x is zero because the zero of a periodic variable is only arbitrary; instead it is the value around which $y_{\text{predicted}}$ cycles, and is called the mesor. The mesor is a measure of central tendency and is superior to the simple mean of all observations because it is not 'pulled' by extra sampling effort at any point around the cycle as any simple mean or mean vector would be. The peak location (value of x at which $y_{\text{predicted}}$ is highest) can be calculated as follows. Where the position of the peak (P_p) is ϑ units after the nominal zero of the cycle (t_0),

$$P_p = t_0 + \vartheta \quad (2)$$

$$\vartheta' = \arctan(B_1/B_2) \quad (3)$$

$$\vartheta = \vartheta' + \text{QC} \quad (4)$$

where QC is a quadrant correction to be added to ϑ' : QC=0 cycles if (B_1, B_2) , treated as (x, y) , are $(+, +)$; QC=0.5 cycles if $(+, -)$ or $(-, -)$, and QC=1.0 cycles if $(-, +)$. A cycle is 2π radians, 360° , etc., and natural cycles are (e.g.) 24 h, 365 days. For any circular variable with k units in a full cycle, the corrections QC_K would be obtained by $\text{QC}_K = (k/360) * \text{QC}_{\text{degrees}}$ and would be governed in the same way by the signs of x and y . To convert ϑ to days of year cycle after the nominal zero (t_0) of the circular scale, multiply by (desired scale/present scale), e.g.

from radians, multiply by $365/2\pi$ for DOY, by $24/2\pi$ for hour in day from radians, etc.

The amplitude is denoted $2A$, where A is the maximum positive or negative departure of predicted y from the mesor, such that the maximum is $B_0 + A$, the minimum is $B_0 - A$, and the entire predicted range, $Y_{\text{max}} - Y_{\text{min}} = 2A$. Thinking of the situation in terms of right triangles, the coefficients B_1 and B_2 (for sin and cos) are the lengths of two sides and A is the hypotenuse (the line joining the origin with the coordinates (B_1, B_2)) and can be calculated (1981) using Pythagoras' theorem:

$$A = (B_1^2 + B_2^2)^{0.5} \quad (5)$$

Often, quite complex variation can be well described as the sum of a few harmonics of a cycle (e.g., dairy data in Bliss, 1958). The periodic aspect of a regression is contained in the pair of parameters for sine and cosine of the transformed periodic x -variable. Additional linear terms, or additional harmonics, or additional non-harmonic cycles can be easily combined (e.g. lunar with annual, tidal with daily) in the same regression. The peak of the contribution of each can be identified. When R' means 'multiply by $2\pi/365$ ' for the conversion of DOY to radians for the annual cycle, and $R_{182.5}$ (or $R'h$ indicating the half cycle) means 'multiply by $2\pi/182.5$ ' for the transformation to radians for the half-annual harmonic, the regression form that includes the second harmonic is:

$$y = B_0 + B_1 \sin(R'DOY) + B_2 \cos(R'DOY) + B_3 \sin(R'hDOY) + B_4 \cos(R'hDOY)$$